GROWTH RATES IN LATITUDINALLY AND VERTICALLY SEPARATED POPULATIONS OF MYTILUS CALIFORNIANUS [1]

PAUL A. DEHNEL [2]

Department of Zoology, University of California, Los Angeles 24, California

Many marine poikilothermal species which encounter a relatively wide temperature difference over a latitudinal or vertical distribution, or over the annual cycle of seasons, demonstrate a compensatory response in various physiological activities. Rao (1953) has shown that the pumping rate of *Mytilus californianus* was higher for northern latitude animals at any given temperature when this activity was compared with southern ones. Segal (1955) compared heart rate of high and low intertidal populations of *Acmaea limatula* and found that low intertidal animals behaved as if they were cold-adapted relative to high intertidal animals. This has also been shown for *Mytilus californianus* for rate of water propulsion (Segal, Rao and James, 1953). These studies suggest a homeostatic tendency in many rate functions. The literature relevant to the problem of acclimation is extensive and has been reviewed recently (see Bullock, 1955 and Prosser, 1955).

With regard to rate of growth, usually, it is assumed that marine poikilotherms which inhabit high latitude seas grow more slowly, grow to a larger size and have a greater longevity, when compared with individuals of the same or closely related species from warmer seas. Such an assumption suggests that rate of growth is a simple function of temperature. Most studies reported in the literature indicate temperature-dependence, and do not, as in the case in metabolic studies, suggest compensation for temperature difference. However, Dehnel (1955) has compared rates of growth of larvae of several species of intertidal gastropods from southeastern Alaska and southern California. These results have shown that northern larvae grew more rapidly at all experimental temperatures, when compared with southern larvae of the same species. A discussion of some of the literature concerning rates of growth and latitude will be found elsewhere (Dehnel, 1955).

The purpose of this study is two-fold: to determine whether rates of growth in populations of the California sea mussel, *Mytilus californianus*, from southeastern Alaska and southern California are adapted in a compensatory direction relative to the temperature difference; to determine the effect of tidal height upon growth rate in this species. Few studies have concerned the latter aspect of any species. Coulthard (1929) compared growth in vertically separated populations of *Mytilus edulis*. These results showed rates of growth to be greater in completely submerged populations. Moore (1934) compared growth in populations of *Balanus*

[1] Aided in part by a grant from the Arctic Institute of North America under contractual arrangements with the Office of Naval Research. The author wishes to express his gratitude to Dr. Theodore H. Bullock, for many helpful suggestions and for critical reading of the manuscript.

[2] Present address: Department of Zoology, University of British Columbia, Vancouver 8, Canada.

balanoides located at different tidal levels, and found that growth was greatest at higher tidal levels except during the first year. Hatton (1938) studied rates of growth in high and low intertidal populations of *Balanus balanoides, Chthamalus stellatus* and *Patella vulgata.* This work revealed that young barnacles located at lower levels grew faster, but older animals grew more rapidly at higher intertidal levels. Reciprocal transplants of high and low intertidal animals showed that lower levels were still unfavorable for growth. Results obtained for *Patella vulgata* indicated that low level populations of this species grew more rapidly when compared with high level ones.

Rates of growth in adults of *Mytilus californianus* were studied by marking and measuring individuals *in situ* in the intertidal and allowing them to remain in the beds, in this manner obtaining natural rates of growth. The period of the study was chosen to be only a limited part of a year, during the growing season.

Material and Methods

Two geographic localities were chosen for this study: Big Rock, Los Angeles County, California (latitude 34° 00′ N., longitude 118° 30′ W.), and Mount Edgecumbe, Alaska (latitude 57° 03′ N., longitude 135° 20′ W.). Time spent at the northern locality extended from June to September, 1952, and July to August, 1953. The mean difference in surface sea water temperature between the two localities during the summer months was about 7° C.

It was regarded as important that rates of size increase in this species be compared at a season when growth was the most rapid. Coe and Fox (1942) showed that mussels from La Jolla, California grew most rapidly during April and May. The temperature of the sea water at that time was about 16° C. Water temperatures around Big Rock, California were not significantly different. In addition to the spring months thus selected for this study, the southern California mussels were measured in November, following the return from the northern locality. In southeastern Alaska it is assumed that comparable conditions for growth occur somewhat later, although no new data justifying this were obtained. In order to show the effect of vertical position upon growth, means of the absolute increase per thirty days in the shell dimensions were plotted as a function of intertidal height (Fig. 4). This plot is presented as it does not seem justified to determine a mean instantaneous relative growth rate value (to be discussed later) for the entire growth period, and the data obtained by Coe and Fox (1942) were desired for comparison.

Big Rock mussels were initially marked and measured April 13, 1952. A second series of measurements was made May 25, 1952 and the last series, November 1, 1952. Mussels were measured in 1954 on the following dates: April 24, May 22, July 1 and July 30. Mussels at Mount Edgecumbe, Alaska were measured on the following dates: June 26, July 24 and September 4, 1952.

Measurements of the shell were used. Individuals were marked by filing an identification mark on the shell and were then allowed to remain in the mussel beds for the period of study. Particular effort was made not to disturb each mussel any more than was necessary. A firm attachment by the byssal threads was confirmed, or the animal was discarded initially. Dial calipers were used for the measurements, which had an accuracy of ± 0.1 mm. The three shell measurements used were the greatest shell length, width and height, except that length was not obtained for the 1952 sample from southern California. About two hundred individuals were measured in Alaska, and a like number in California.

To compare rates of growth of an attached species from different localities, it is necessary to locate groups of animals that occupy approximately comparable intertidal positions, with respect to wave action, degree of tidal exposure, compactness of the beds and size of animals that compose the bed. These parameters were difficult to measure, and assurance of ecologically similar conditions could be made only in a subjective way. The mussel beds at Mount Edgecumbe, Alaska and Big Rock, California were exposed directly to the open surf; the size of the animals was about the same (southern populations were somewhat larger); the mussel beds at the two localities were about the same in numbers of individuals per given area. On the causeway at Mount Edgecumbe, which consisted of a constructed road that served to connect several islands, and projected into the open ocean, the ecological distribution of *Mytilus californianus* was somewhat different from that observed at Big Rock. The intertidal zone is essentially vertical, and the gently sloping rocky coast so characteristic of southern California is lacking. Hence, it was necessary to attempt to locate mussel beds on a nearly vertical substratum that would be comparable, intertidally, to mussel beds in the south that had much greater horizontal distribution. The mussels in southern California were located at the 3.0 ft. ($\pm$ 0.5 ft.) and 1.0 ft. ($\pm$ 0.5 ft.) tide level and those in Alaska, at the 5.5 ft. ($\pm$ 0.5 ft.) level (zero datum level is mean lower low water). The lower figures demark the lower level of vertical distribution of this species at the respective localities. It should be noted that at both localities populations of *Mytilus californianus* were distributed vertically in the intertidal to well-delineated levels, below and above which the populations were essentially non-existent. This does not take into account subtidal populations recently located on the southern California coast (Berry, 1953; Rao, 1953). Values given elsewhere in the text for hours and percentage exposure per week at these levels were calculated from Ricketts and Calvin (1952, Fig. 112).

Under field conditions the problem of recovery of marked animals was serious. Within one month there may occur a great deal of settling of barnacle larvae, young mussels and seaweed, thus obscuring marked animals. Some individuals moved along or within the bed. This movement may be over the surface of the bed, or, as in many cases, mussels moved vertically from the surface of the bed several inches down to the rock substratum. One month following a series of measurements, about 60% recovery was realized and two months later, approximately 40% of the remainder. At lower intertidal levels in southern California about 80% returns were obtained over the period of four months. It is assumed that the losses were non-selective with respect to the size of the animals.

Method of Analysis

As yet no adequate formula has been propounded to describe all phases of growth in any animal (Weymouth, McMillan and Rich, 1931; Huxley, 1932; Brody, 1945). For this material the most suitable expression is the instantaneous (true) relative growth rate $(k) = \frac{dL/dt}{L}$. A discussion of the significance and justification for using this method will be found elsewhere (Dehnel, 1955). The

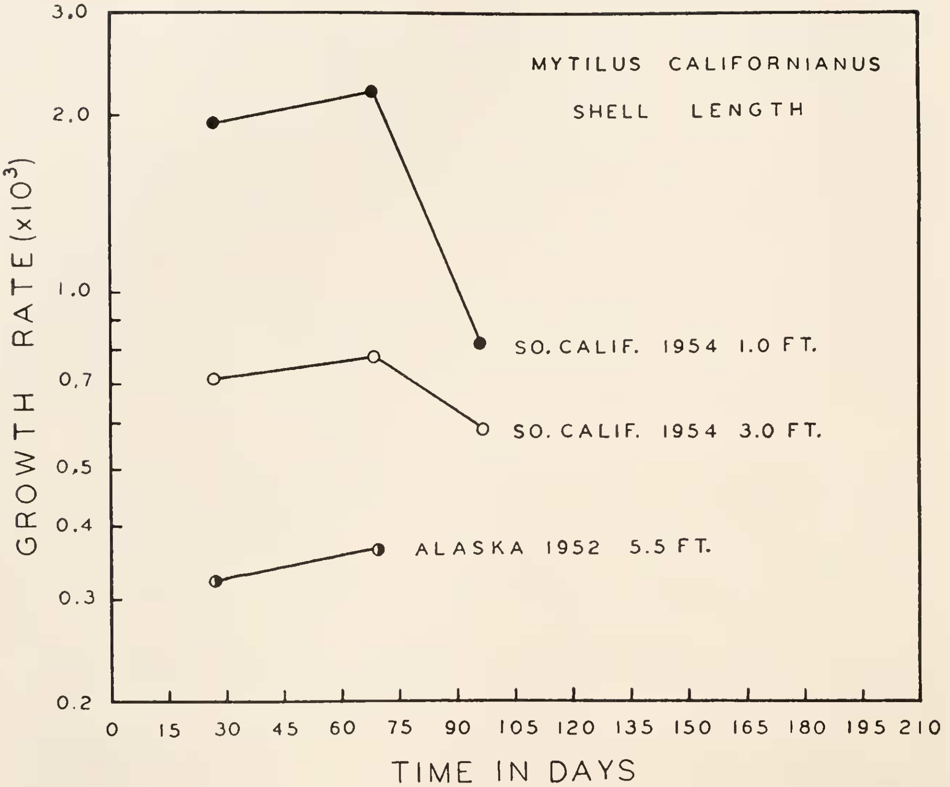

FIGURE 1. A comparison of the rate of growth in length of shell in populations of *Mytilus californianus* from Mount Edgecumbe, Alaska at one intertidal level, and Big Rock, California at two intertidal levels. Each point represents the mean *k* value for a sample of fifty or more individuals. The initial value is plotted on the day at which the second measurement was made.

instantaneous relative growth rates of the length, width and height of the shell were plotted as a function of time (Figs. 1, 2, 3). The initial value is plotted on the day at which the second measurement was made.

The means of the initial length, width and height of the shell are about 25% greater for the southern California mussels sampled than for northern ones. Presumably, similar size in latitudinally separated populations of a given species indicates different chronological ages, the northern ones being older (Wimpenny, 1941). Hence, samples of the northern and southern populations under consideration should be approximately the same age. A small initial size was chosen, as growth rates are more rapid in young animals.

RESULTS

Growth rate in latitudinally separated populations

When the instantaneous relative growth rate of the length of the shell is plotted as a function of time (days), it is seen that the rate of linear size increase of this dimension is greater in the population from southern California at the 3.0 ft. level (Fig. 1) than in the Alaskan one (5.5 ft. level). The rate of the northern sample is about 45% of the southern one, initially, but the slopes of the two curves are nearly parallel. The mean absolute increase per thirty days for the southern California sample over the period from April 24 to July 30, 1954 was 0.96 mm.; for the smaller mussels from Alaska (June 26 to September 4, 1952), the increase was 0.33 mm. In the middle part of the summer, the rate for the southern sample de-

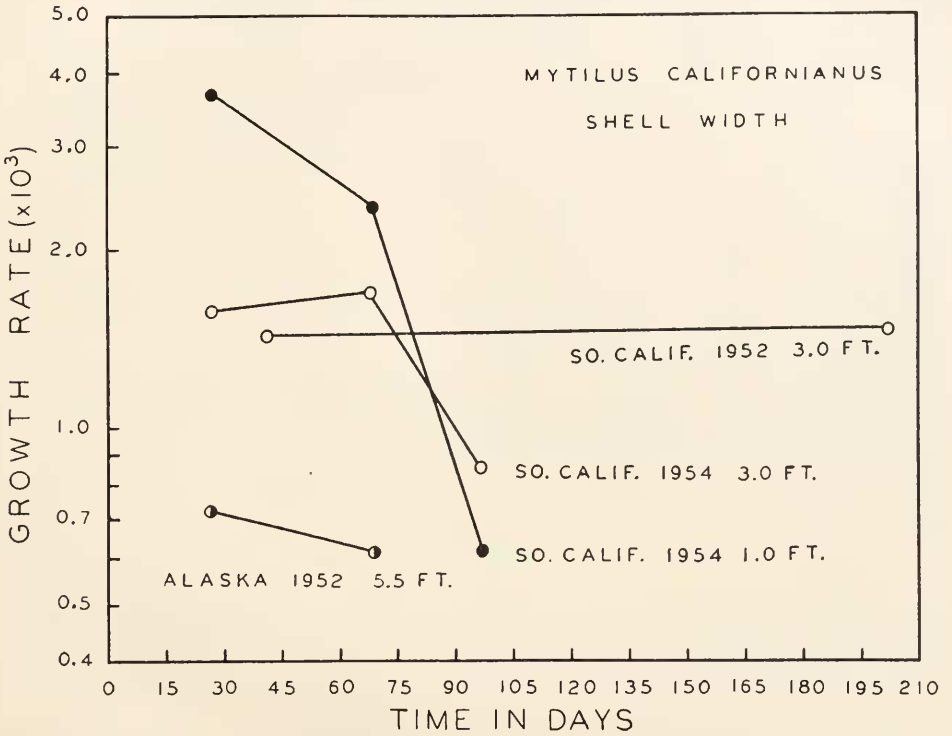

FIGURE 2. A comparison of the rate of growth in width of shell in populations of *Mytilus californianus* from Mount Edgecumbe, Alaska at one intertidal level, and Big Rock, California at two intertidal levels. Each point represents the mean k value for a sample of fifty or more individuals. The initial value is plotted on the day at which the second measurement was made.

creases, but is still growing at a rate greater than the one from Alaska, as seen from an extrapolation of the northern curve.

Also, the rate of linear increase in shell width is greater in the population from the 3.0 ft. level from southern California when compared with the population at the 5.5 ft. level from Alaska (Fig. 2). The rate of the northern sample, again, is about 45% of the southern one. The initial rates of the two samples from southern California are very similar. The 1952 sample shows no decline in rate due to the lack of intermediate points. For the years 1952 and 1954 the mean absolute increase per thirty days was 0.90 mm. and 0.81 mm., respectively. The mussels from Alaska showed a 0.30 mm. increase for the same length of time.

With regard to shell height the growth rate for the southern sample is greater (Fig. 3). Comparing the 1954 sample from southern California (3.0 ft.) with the Alaskan one, there is essentially no difference between the initial rates. However, subsequent segments of the curve show that the northern sample is decreasing its rate to a greater extent. The 1952 sample from southern California at the same intertidal level has a rate which is about 46% of the Alaskan group. The increase per thirty days for shell height was 0.85 mm. in 1952 and 0.69 mm. in 1954 for the sample from southern California, and 0.34 mm. for the northern one.

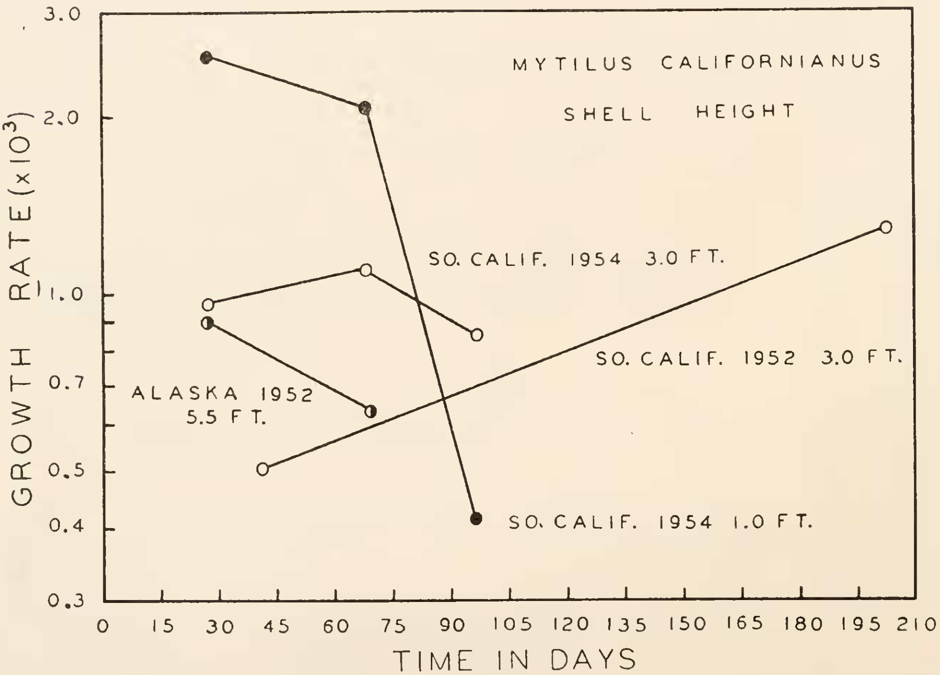

FIGURE 3. A comparison of the rate of growth in height of shell in populations of *Mytilus californianus* from Mount Edgecumbe, Alaska at one intertidal level, and Big Rock, California at two intertidal levels. Each point represents the mean *k* value for a sample of fifty or more individuals. The initial value is plotted on the day at which the second measurement was made.

It is evident from Figures 2 and 3 that the line drawn between the two *k* values (which represents the second and third measurements, May 25 to November 1, 1952) of both width and height of the populations from southern California (3.0 ft.) does not describe the conditions of linear increase in shell dimensions because of a lack of intermediate points. As a result, a more refined comparison might be made between the first two points on the curve (April 13 to May 25, southern California; June 26 to July 24, Alaska). Absolute increase in shell width for southern mussels was 0.86 mm. per thirty days, and for northern ones 0.32 mm. Increase in shell height for southern animals was 0.64 mm. per thirty days, and 0.43 mm. for northern ones. These latter values differ somewhat from the initial ones, because of the inclusion of more animals recovered at the second measurement. Relative rate (k) values have been determined for each individual of both populations, and then a mean rate calculated. Standard deviation for each rate was obtained, and a test was made to determine the significance of the difference between the two means (Alaska and southern California) when the population standard deviations are known. The mean rates for shell width are as follows: Alaska, $k = 0.00081$ ($\pm$ 0.00055); southern California, $k = 0.00170$ ($\pm$ 0.00166). The difference between these two means is significant ($P < 0.002$). Values for shell height are as follows: Alaska, $k = 0.00111$ ($\pm$ 0.00083); southern California, $k = 0.00142$ ($\pm$ 0.00107). The difference between these two means is insignificant ($P = 0.100$); such differences could occur by chance alone 10% of the time. A comparison of the mean rates (k) for length of shell between Alaskan and southern California mussels (3.0 ft.) shows them to be statistically significant ($P < 0.002$).

Comparison of the absolute increase per thirty days and/or the relative rate of increase of linear size between the 1952 and 1954 samples from southern California at the 3.0 ft. level is of value. This comparison points out the similarity of linear increase for two years in this population and is suggestive that the values obtained are characteristic of rates of increase of animals from this locality. These values also suggest that sea water temperatures were similar, which they were, and that the amount of plankton available was similar.

From these data, it would appear that the rate of size increase in shell length and width is greater in the sample of mussels from southern California than in that from Alaska, but the increase in shell height, though greater, cannot be said to be significantly different on these data. This means the shells are also growing differently shaped in the two populations.

Growth rate in vertically separated populations

During the spring and summer of 1954 not only were mussels studied at the 3.0 ft. tide level, but also at the 1.0 ft. level. The purpose of this was to determine the effect of intertidal height on the rate of linear increase of shell dimensions in this species. Reference to Figure 4 shows the differences in absolute increase in all shell dimensions per thirty days as it varies with tidal height. Data from Coe and Fox (1942) are included on this graph in order to illustrate the increase in mussels from La Jolla, California that were totally submerged. A comparison between populations located at the 1.0 ft. and the 3.0 ft. tidal levels from southern California indicates the great effect submergence has upon growth in this filter-feeding invertebrate.

Inspection of the data shows that the absolute increase in shell length at the 1.0 ft. level is over two times that at the 3.0 ft. level (2.3 mm./0.96 mm.), for a thirty-day period. With respect to width, the difference is not so great (1.3 mm./0.90 mm., 1952; 0.81 mm., 1954). An average of the last two values shows the mean increase of the higher level to be about 66% of the lower one. Absolute increase in height is about the same as the width relationship (1.2 mm./0.85 mm., 1952; 0.69 mm., 1954). An average of these values shows the 3.0 ft. animals to increase about 64% of the 1.0 ft. mussels.

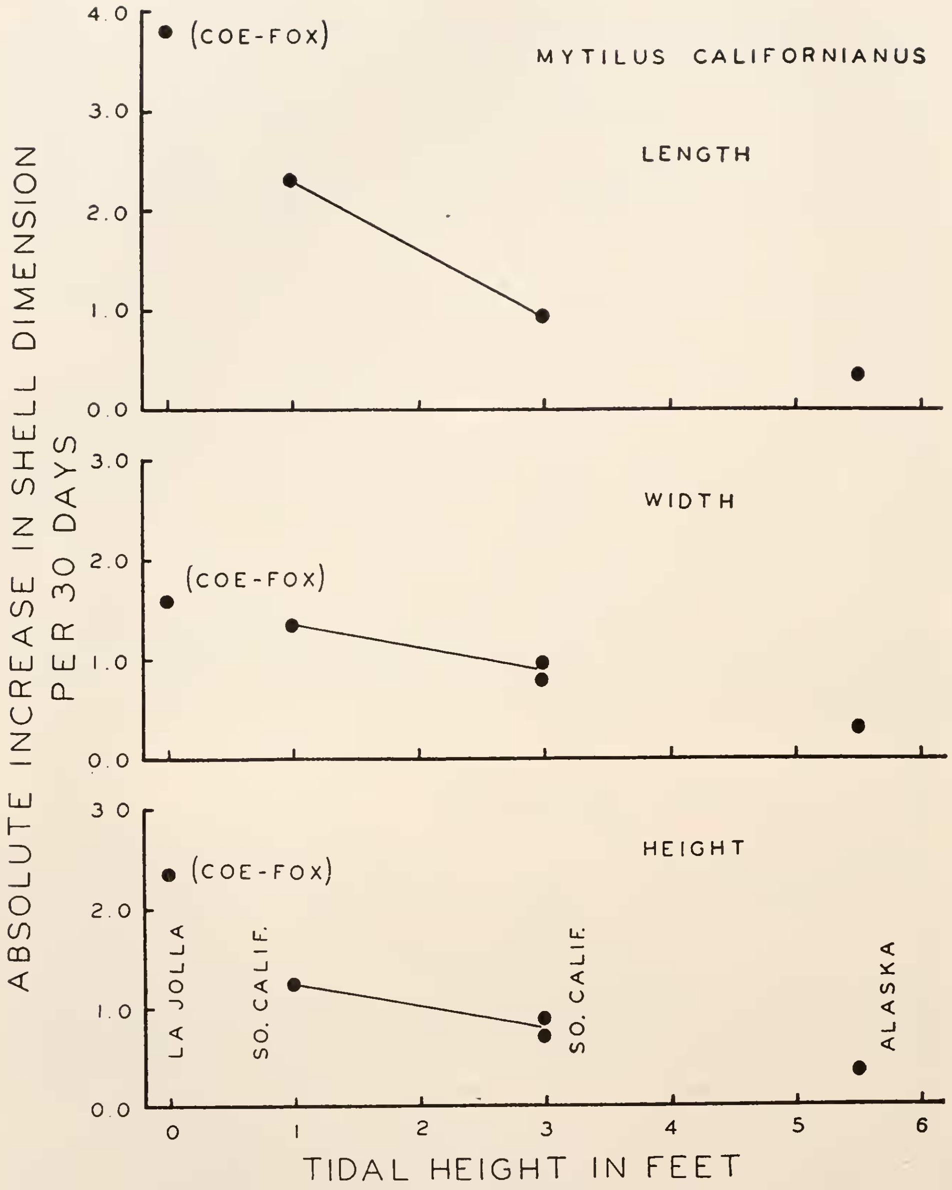

FIGURE 4. A comparison of the absolute increase in shell dimensions per thirty days as a function of intertidal height in populations of *Mytilus californianus* from La Jolla, California, Big Rock, California and Mount Edgecumbe, Alaska. Data for La Jolla mussels were obtained from Coe and Fox (1942, page 7, Table 1). Each point represents the mean increase for a sample of fifty or more individuals.

Discussion

It would be well to mention at the outset that the data presented by Coe and Fox (1942) for growth of mussels at La Jolla, California, under totally submerged conditions are in relative agreement with rates obtained at Big Rock, California, at the 1.0 and 3.0 ft. tide levels. In their paper, Coe and Fox (1942) present length measurements, and ratios from which width and height measurements may be obtained. Their ratios of W/L = 0.37 and H/L = 0.5 are not in agreement with the ones from Big Rock at either tidal level. However, there is no reason to believe that populations of mussels under entirely different ecological conditions should have the same growth ratios as ones submerged completely. Such mussels would conceivably compare only with subtidal populations of mussels, and even then growth might be much different.

The most obvious difference between populations of mussels from Big Rock at the 3.0 ft. and the 1.0 ft. tide levels is the degree of submergence per given period of time. Mussels located at the 3.0 ft. level were submerged about 58% of the time (14 hours per day), and ones from the 1.0 ft. level were submerged about 88% or twenty-one hours per day. It may be assumed that mussels obtain food in proportion to their access to it, *i.e.*, to their time of submergence. Rao (1954) has adduced good evidence for this. Then it may be expected that the food intake of the 1.0 ft. mussels compares with that of the 3.0 ft. ones as 88:58 or 100:66. If it is assumed that no difference existed in available food material per liter of sea water between the two populations at Big Rock, the difference between rates of linear increase in these two populations is partly explained.

The significance of vertical distribution as it affects rates of linear increase in species such as *Mytilus californianus* becomes apparent when mussels from southern California and Alaska are compared. Previously, it was stated that one population of Big Rock mussels was located at the 3.0 ft. tide level. These animals are able to filter approximately fourteen hours per day. Mussels from the population studied in Alaska were located at the 5.5 ft. tide level. They were able to filter about ten hours per day. The Big Rock mussels are submerged 1.4 times longer per twenty-four hours than the Alaskan ones. Even though the degree of submergence differs in the two populations, it is felt that mussels located at the 5.5 ft. level in Alaska are ecologically equivalent to ones from Big Rock at the 3.0 ft. tide level.

From values given by Rao (1953) pumping rates as a function of weight of soft parts for mussels from different latitudes may be determined. Weights of animals used were nearly the same (northern mussels have heavier shells relative to body weight), and by taking into account latitudinal acclimation, Big Rock mussels (16° C.) filter about two liters per hour, those from Alaska (10° C.), about one liter per hour. If the available organic matter per liter of sea water for northern and southern waters is the same, Big Rock mussels would filter $1.4 \times 2 = 2.8$ times as much food as the higher intertidal and only partially acclimated Alaskan sample. The relative growth rates (k) were found to be in the ratio 2:1 for length, 2:1, width and 1.3:1 for height. We may attempt to estimate the expected rate of linear growth in shell dimensions of Alaskan mussels if they were submerged to the same extent as the ones from Big Rock located at the 3.0 ft. level. Volume change must be calculated and this converted into linear increase. The ratio of food obtained is 2.8 and its cube root is 1.41. The value thus found gives the ratio of expected fourteen hour to observed ten hour increase in length, width or height for Alaskan mussels. Also, this value (1.41) may be compared with the growth rate ratios given above. Considering the roughness of the estimate, the agreement is good and suggests that there is acclimation of growth rate.

If the interpretation presented is valid, and part of it is based upon the assumption and belief that the northern mussels are ecologically equivalent to lower intertidal southern ones, it could then be stated that even though relative rates in a population of *Mytilus californianus* from southern California are greater, mussels from Alaska, if chosen from a level with the same periods of submergence, would grow at approximately the same rate in spite of the lower temperature.

Summary

1. Rates of growth have been studied in populations of *Mytilus californianus* collected from southern California and southeastern Alaska. As nearly as possible natural rates of growth have been determined from populations in the field.

2. Length, width and height of the shell are used as criteria for determining rates of growth in this species. Comparisons of rates of growth between northern and southern populations are made by the use of relative rate (k) values.

3. Mussels were measured at the 1.0 ft. and 3.0 ft. tidal levels in southern California and the 5.5 ft. level in Alaska.

4. Rates of growth of *Mytilus* are found to be greater in the sample from southern California, comparing the 3.0 ft. level, than in that from Alaska. However, it was found that the southern California population is submerged for a greater period of time per week. The greater period of submergence and the greater weight of soft parts for a given shell size, recently shown by Rao (1953) for the southern population, mean a greater food intake in spite of acclimation of pumping rate. Attempts to correct for these factors suggest that the actual discrepancy in intrinsic growth rate is small or absent. In particular, Rao's findings give reason to believe that the heavier bodied southern mussels lay down no more shell length per unit of body weight than comparable northern ones.

5. Comparison of relative rates of growth in vertically separated populations of this species shows a large positive effect of submergence upon rate of increase of shell dimensions.

LITERATURE CITED

Berry, S. S., 1953. On the supposed stenobathic habitat of the California sea-mussel. *Calif. Fish and Game*, **40**: 69–73.

Brody, S., 1945. Bioenergetics and growth. Reinhold Publishing Corp., New York.

Bullock, T. H., 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.*, **30**: 311–342.

Coe, W. R., and D. L. Fox, 1942. Biology of the California sea-mussel (*Mytilus californianus*). 1. Influence of temperature, food supply, sex and age on the rate of growth. *J. Exp. Zool.*, **90**: 1–30.

Coulthard, H. S., 1929. Growth of the sea mussel. *Cont. Canadian Biol. and Fish.*, **4**: 123–136.

Dehnel, P. A., 1955. Rates of growth of gastropods as a function of latitude. *Physiol. Zool.*, **28**: 115–144.

Hatton, H., 1938. Essai de bionomie explicative sur quelques espèces intercotidales d'algues et d'animaux. *Annales de L'institut Océanographique*, **17**: 241–348.

Huxley, J. S., 1932. Problems of relative growth. Lincoln Mac Veagh, the Dial Press, New York.

Moore, H. B., 1934. The biology of *Balanus balanoides.* I. Growth rate and its relation to size, season and tidal level. *J. Mar. Biol. Assoc.,* **19**: 851–68.

Prosser, C. L., 1955. Physiological variation in animals. *Biol. Rev.,* **30**: 229–262.

Rao, K. P., 1953. Rate of water propulsion in *Mytilus californianus* as a function of latitude. *Biol. Bull.,* **104**: 171–181.

Rao, K. P., 1954. Tidal rhythmicity of rate of water propulsion in *Mytilus,* and its modifiability by transplantation. *Biol. Bull.,* **106**: 353–359.

Ricketts, E. F., and J. Calvin, 1952. Between pacific tides. Stanford University Press, Stanford, California.

Segal, E., 1955. Microgeographic variation as thermal acclimation in an intertidal gastropod. Ph.D. dissertation, Univ. of California, Los Angeles.

Segal, E., K. P. Rao and T. W. James, 1953. Rate of activity as a function of intertidal height within populations of some littoral molluscs. *Nature,* **172**: 1108–1111.

Weymouth, F. W., H. C. McMillan and W. H. Rich, 1931. Latitude and relative growth in the razor clam, *Siliqua patula. J. Exp. Biol.,* **8**: 228–249.

Wimpenny, R. S., 1941. Organic polarity: some ecological and physiological aspects. *Quart. Rev. Biol.,* **16**: 389–425.